Calcium Usage by Turfgrasses: The Nutrient Forgotten by Turf Managers

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Of the six macronutrient elements required by all vascular plants, calcium (Ca) is probably the most forgotten by turf managers and horticulturists. Calcium is a major component of most liming materials. Therefore, if soil pH is adjusted through the use of lime, Ca is automatically applied and will be present in relatively large amounts. Where soils are already neutral or alkaline, Ca is frequently part of the soil's parent mineral matter and thus present in abundance. Consequently, during the normal management of landscaped sites, Ca will be present naturally or applied as lime. So, you might ask, is Ca availability ever a problem that requires attention? In most soil-based cultural systems, the answer is no.

However, increasingly plants are being maintained in the landscape on synthetic media. On the golf course, USGA specification greens are essentially a sand culture which provides almost no Ca. Because such media are largely silicon based and have a low cation exchange capacity, little exchangeable aluminum or manganese will be present and exchange acidity rarely becomes a problem. Even if the pH is low, it will rarely negatively affect plant growth. Plants maintained in containers or in deep mulch may contact little if any soil and thus have a limited supply of calcium. In urban settings, roof-top gardens or landscapes are maintained in artificial media from which soil is excluded because of its weight. Here again, no natural supply of Ca may be available.

Greenhouse managers also use soil-less mixes but they are familiar with potential Ca deficiency problems and often add lime while preparing their mix. The complex fertilizer blends used for greenhouse crops also normally contain Ca since it, along with most other nutrients, might not be present in the synthetic culture medium.

Turf managers increasingly are required to grow turf on reclaimed or drastically modified land where the Ca content might be very low. Turf nutrition problems on greens and tees can be aggravated by the low height of cut which discourages deep rooting and makes the grass plants dependent on a limited medium volume. It is not unusual for turf managers to operate in situations where plant nutrition must be considered beyond the traditional use of nitrogen, phosphorus and potassium.

Tissue Content and Supply

Leaves of most turfgrasses contain sufficient amounts of Ca when it is present at between 5.0 and 12.5 g/kg (0.5 to 1.25%) of dried tissue. This is about the same concentration as that of phosphorus (P) which was earlier reviewed in this series on turfgrass nutrition. Like P and most mineral nutrients, the concentration of Ca can change significantly during the growing season. Hall and Miller observed the Ca content of field-grown Kentucky bluegrass clippings to vary between 0.82 and 1.47% on a dry weight basis. Calcium levels appeared to be highest when rapid root growth was likely, in early summer and mid-late fall. When shoot growth is rapid, leaf Ca becomes diluted and the tissue concentration declines.

However, unlike P, Ca is abundant in the solution of most soils. In fertile soils, it is the dominant cation on the cation exchange complex. This results in a soil water Ca concentration of about 1.6 mM (64 ppm) in a normal fertile soil. However, because Ca is absorbed by roots at a rate considerably less than that of the water in which it is dissolved, the Ca tends to be 'filtered' out of solution at the root surface and accumulates in the rhizosphere (zone of soil adjacent to a root) to concentrations greater than 70 mM (2800 ppm). Consequently, the uptake of Ca by plant roots occurs as a largely passive process while the uptake of phosphate is strongly active. For a review of the characteristics of Ca in soil and the action of

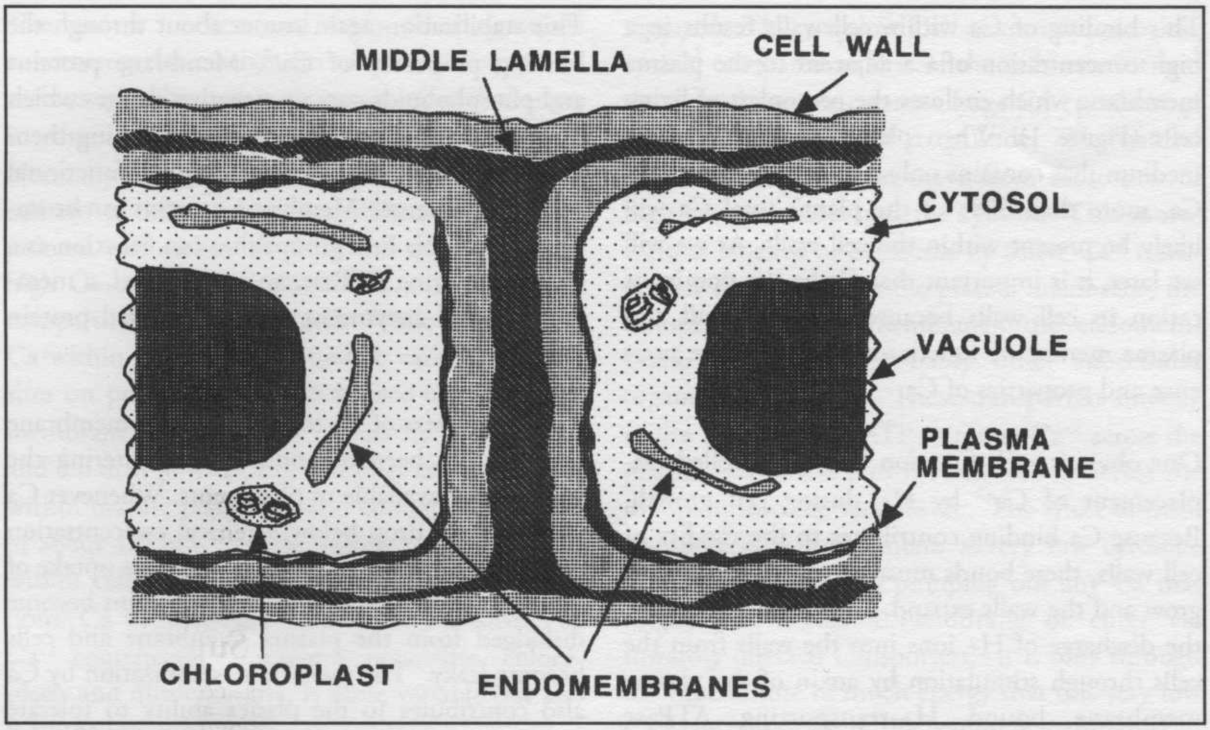

Figure 1. Distribution of calcium within plant cells. The darker the shading, the more concentrated is the free ionic calcium.

liming materials, please consult an earlier *TurfGrass TRENDS* article (Hull 1995). In this article, I will concentrate on the roles played by Ca in the growth of turfgrass plants and on how this information might be useful to the turf manager.

Ca Deficiency Symptoms Are Linked To Its Role In Cell Wall Synthesis

When most plants experience a Ca deficiency, the first visible symptom is a cessation of shoot and root growth. This can occur within a few hours of withholding Ca and becomes most apparent at the growing points. The reason for this is linked to the role of Ca in stabilizing developing cell walls. At growing points (apical meristems) newly formed cells generate a cell wall from complex long-chain carbohydrates (polysaccharides) produced within the cells and excreted into the extracellular space between cells. This material is gel-like and has no structure. However, the very first wall materials produced contain large numbers of organic acid groups (polyglacturonic acid = pectates) which carry negative charges. These charges attract positively charged cations and give to the cell wall a large cation exchange capacity. Because of its abundance in most soils, Ca^{+2} ions normally balance many of these cell wall negative charges. Because of its double charge, Ca^{+2} ions have the capacity to link two pectate chains together which gives some organization and rigidity to the new cell walls. It is likely that when later cell wall polysaccharides (hemicelluloses, cellulose) are released from the cells, they utilize these initial pectin chains to establish the structure of the primary cell wall. It is clear that if Ca is not present, normal cell wall structure is not established and an organized tissue cannot develop.

The amount of Ca bound to cation exchange sites in cell walls depends on the number of exchange sites present and the availability of Ca to the root. Thick walled cells contain more exchange sites and will bind more Ca. This is typical of many broad leafed plants (dicotyledons) which normally have thick roots and contain more Ca than the fine rooted grass-like plants (monocotyledons) which generally contain less Ca. These differences in cell wall structure and volume partially explain why monocotyledons normally require less Ca than do dicotyledons.

This binding of Ca within cell walls results in a high concentration of Ca adjacent to the plasma membrane which encloses the protoplast of living cells (Figure 1). When plants are growing in a medium that contains only a moderate amount of Ca, more than 50% of the plant's total Ca will likely be present within the cell walls. As we will see later, it is important that Ca be the dominant cation in cell walls because both cell wall and plasma membrane functions depend on the presence and properties of Ca.

One obvious such function is the controlled displacement of Ca^{+2} by H+ during cell growth. Because Ca binding contributes to the rigidity of cell walls, these bonds must be relaxed when cells grow and the walls expand. This comes about by the discharge of H+ ions into the walls from the cells through stimulation by auxin of the plasma membrane bound H+-transporting ATPase (Figure 2). The excess H+s exchange for some of the bound Ca^{+2}s breaking the Ca linkages between pectin chains and allowing the chains to slide apart and the walls to expand. After wall expansion, the excess H+s are dissipated and Ca bonds become reestablished again helping to stabilize and strengthen the wall. There is more involved than what is described here but this interaction between wall acidification and Ca-bond breaking is reasonably well established.

Ca Stabilizes Plasma Membrane Structure

As indicated above, the presence of relatively high Ca levels within plant cell walls is critical for proper plasma membrane function. All biological membranes consist of a phospholipid core in which numerous proteins are inserted. These protein globs can float around laterally in the membrane, which is of a liquid consistency, and make contact with each other. In order for these membrane proteins to function as an ion transporter or provide a pore for water conduction into the cell, the component parts must come together and function as a unit. Since these component proteins are free to move about, there interactive structure must be stabilized for them to carry out a physiological function.

This stabilization again comes about through the binding properties of Ca^{+2}. Membrane proteins and phospholipids contain negative charges which can bind with Ca^{+2} in specific ways linking them together and thereby stabilizing a functional complex structure. Membrane proteins can be stabilized by Ca^{+2}s into groups that can function as a H+-transporting ATPase, an ion channel, a membrane-bound enzyme or other functional protein assemblages.

The uniqueness of Ca to carry out this membrane function has been demonstrated by altering the Na/Ca ratio available to plant roots. Whenever Ca is allowed to drop below a critical concentration relative to other cations, transmembrane uptake of nutrient ions is inhibited, surface proteins become dislodged from the plasma membrane and cells become leaky. The membrane stabilization by Ca also contributes to the plant's ability to tolerate high salt concentrations.

LaHaye and Epstein found that bean plants grown in the presence of abundant Ca were protected from injury by salt levels (50mM NaCl) that would seriously inhibit the growth of low Ca plants. It is a general practice in irrigated agriculture to protect crops from injury due to poor quality irrigation water by increasing the Ca content of the root zone. Adequate Ca levels in the soil make plants more tolerant of many physical and biological stresses.

Calcium as a Signal Messenger

For a little more than ten years, it has been recognized that Ca plays a critical role in a process that has baffled biologists for many years. It has long been known that plants can respond to environmental stimuli or signals such as day length, low temperature, pathogen attack, toxic metals, etc. The plant response is often a reaction which enables the plant to increase its tolerance to a stress condition or to respond in a manner which favors its survival. What has not been clear is exactly how the perception of a stimulus is transmitted into an appropriate response. How does the presence of a pathogenic fungus tell the plant to take defensive measures? How is an elevated auxin level translated into accelerated stem growth?

The answer to these and many other questions concerning the mechanism of plant responses to various stimuli appears to center around changes in the internal Ca^{+2} concentration of cells. Normally, there are great differences in the Ca^{+2} content of cell compartments (Figure 1). As was pointed out earlier, the cell wall normally has a high Ca content and this is also true for several compartments inside the cell. While much of the Ca within cell walls is bound to cation exchange sites on pectin and on the surface of the plasma membrane, free ionic Ca^{+2} levels are between 0.1 and 1.0 mM (4-40 ppm). The large central vacuole within mature plant cells also contains Ca^{+2} levels of about 1.0 mM and the endomembrane system within cells may contain as much as 50 mM (2 ppm) Ca with free Ca^{+2} present at 3-4 mM. The Ca^{+2} content of cytoplasmic organelles, chloroplasts and mitochondria, is quite variable but also is in the low mM range.

By comparison, the cytosol (fluid matrix of the cell's cytoplasm) contains very low concentrations of free Ca^{+2} ions; typically 0.1 mM or 0.004 ppm although values as low as 0.03 mM have also been reported. This very low Ca^{+2} concentration in the cytosol compared to that of the cells exterior and the central vacuole creates a huge Ca^{+2} gradient of three to four orders of magnitude. The natural tendency is for Ca^{+2} to move from those sites of high concentration into the cytosol. This movement is blocked or overcome by active Ca^{+2} transporters that operate in the plasma membrane, the tonoplast (vacuolar membrane), the endomembrane system and probably other subcellular organelles (Figure 2). These transporters directly utilize the energy in ATP to pump Ca^{+2} across the plasma membrane into the cell wall or across the tonoplast into the vacuole etc. The effect of these transporters is to maintain a very low cytosolic Ca^{+2} concentration by pumping out any Ca that might leak across a membrane or enter via inwardly directed transporters. It is only through the expenditure of much energy that this very low Ca^{+2} concentration in the cytosol is maintained.

Why is maintaining a low cytosolic Ca^{+2} content important? One reason is to prevent Ca from precipitating phosphate which is essential for just about every metabolic pathway. Remember it is in

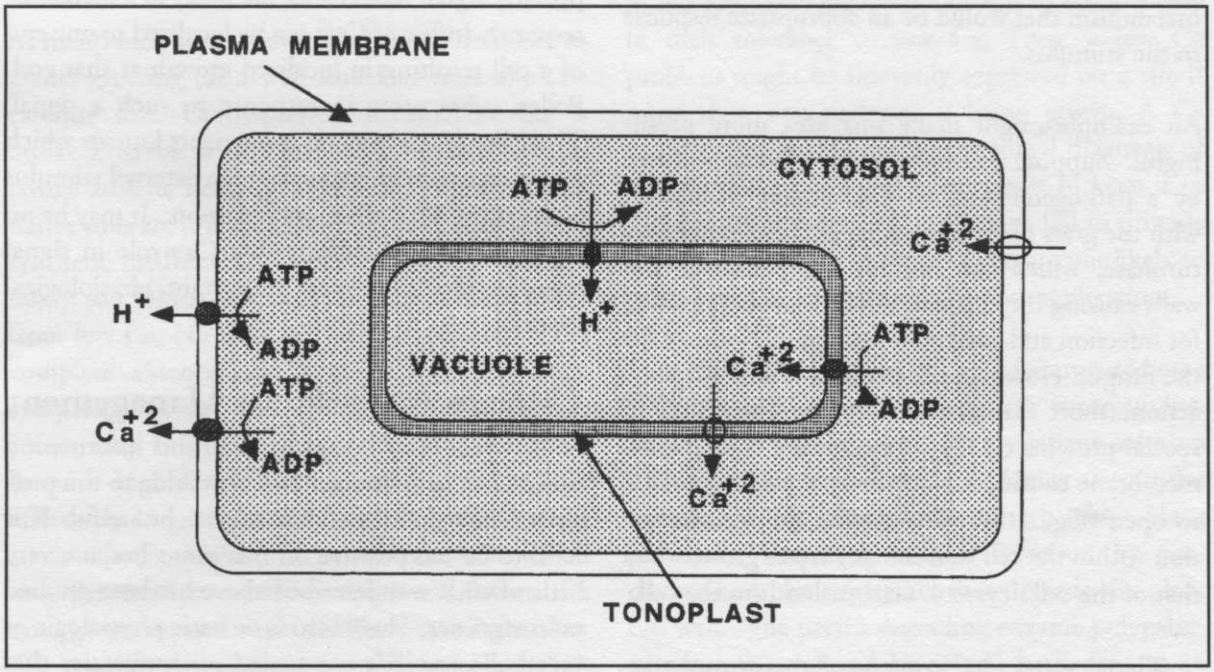

Figure 2. Major active transporters involved in pumping Ca and H out of the cytosol and passive Ca channels used to permit Ca to reenter the cytosol.

the cytosol that many basic metabolic processes occur in total or in part and free phosphate (Pi) is needed for most of them. Also free magnesium ions (Mg^{+2}) are required for most reactions involving ATP and Pi and most metabolic pathways contain several such reactions. Calcium^{+2} can compete with Mg^{+2} for enzyme binding sites rendering the enzyme inactive. Consequently it is not healthy to have high concentrations of Ca^{+2} around where reactions involving ATP, Pi or Mg^{+2} are supposed to be occurring.

Once having established this sharp difference in Ca^{+2} concentration between the cytosol and its surroundings, signal transduction mechanisms have evolved which utilize the partial collapse of this Ca^{+2} gradient. Signal transduction involves the conversion of a stimulus (signal) to a chemical reaction in the cell which can directly or indirectly initiate a metabolic change or response to that stimulus. Such a signal transduction system must be rapid and require the expenditure of no energy. Otherwise a cellular response might be too late or it might be too easily blocked by degrading the energy source. If a stimulus causes a rapid influx of Ca^{+2} into the cytosol, it can trigger a series of new reactions which in turn could cause a shift in metabolism that would be an appropriate response to the stimulus.

An example might make this idea more meaningful. Suppose a turfgrass plant is being attacked by a pathogenic fungus. The fungus in contact with the grass plant releases an enzyme, polygalacturonase, which can degrade the pectin of cell walls causing the tissue to weaken, provide a route for infection and supply an interim food source for the fungus. However, the product of this enzyme's action, short carbohydrate chains, can bind to special proteins on the surface of the cell's plasma membrane causing Ca channels in the membrane to open (Figure 3). Because the Ca^{+2} concentration within the cell wall is many times greater than that of the cell's cytosol, Ca^{+2} rushes into the cell.

The elevated Ca^{+2} content of the cytosol triggers certain specific reactions. Calcium can bind with an existing protein kinase enzyme which is then activated to add a phosphate from ATP to other enzymes thereby either activating or inactivating them. This change in enzyme activity will shift metabolism along different pathways from where it had been proceeding earlier. In this case, metabolism may be shifted to produce phenolic compounds which are toxic to fungi and thereby prevent infection. Alternatively, the higher cytosolic Ca^{+2} level may cause four Ca ions to bind with a regulator protein such as calmodulin which in turn binds with specific enzymes either activating or inhibiting their function (Figure 3). Calmodulin-Ca_4 can bind with the enzyme NAD kinase activating it to phosphorylate NAD to form NADP. NADP is required in the pathway that produces phenolic compounds so it complements and reinforces the effect of the protein kinase described earlier. Calmodulin-Ca_4 may also bind with the plasma membrane Ca-translocating ATPase activating it to pump more Ca^{+2} out of the cytosol into the cell wall and restoring the cytosol to its original low Ca^{+2} level.

In this example, the elevated Ca^{+2} in the cytosol served as a second messenger (short chain carbohydrates generated by the fungus in the cell wall being the primary messenger) which linked the primary signal received by the plant to a metabolic response. Influx of Ca^{+2} can be localized to one end of a cell resulting in localized growth at that end. Pollen tubes grow in response to such a signal. There are several second messengers known which promote a cellular response to an external stimulus but by far Ca^{+2} is the most common. It may be no exaggeration to conclude that Ca's role in signal transduction is its most important physiological function.

Calcium in Turfgrass Management

By now you may be asking if all this information on Ca and its functions is of any value to the turfgrass manager. I believe it might be useful. It is hard to be too positive on this point because very little of what was described above has been studied on turfgrasses. There is so little basic physiologic or metabolic research conducted on turfgrasses that we have little choice but to extrapolate from research involving other plants. However, the above story has been established for several very

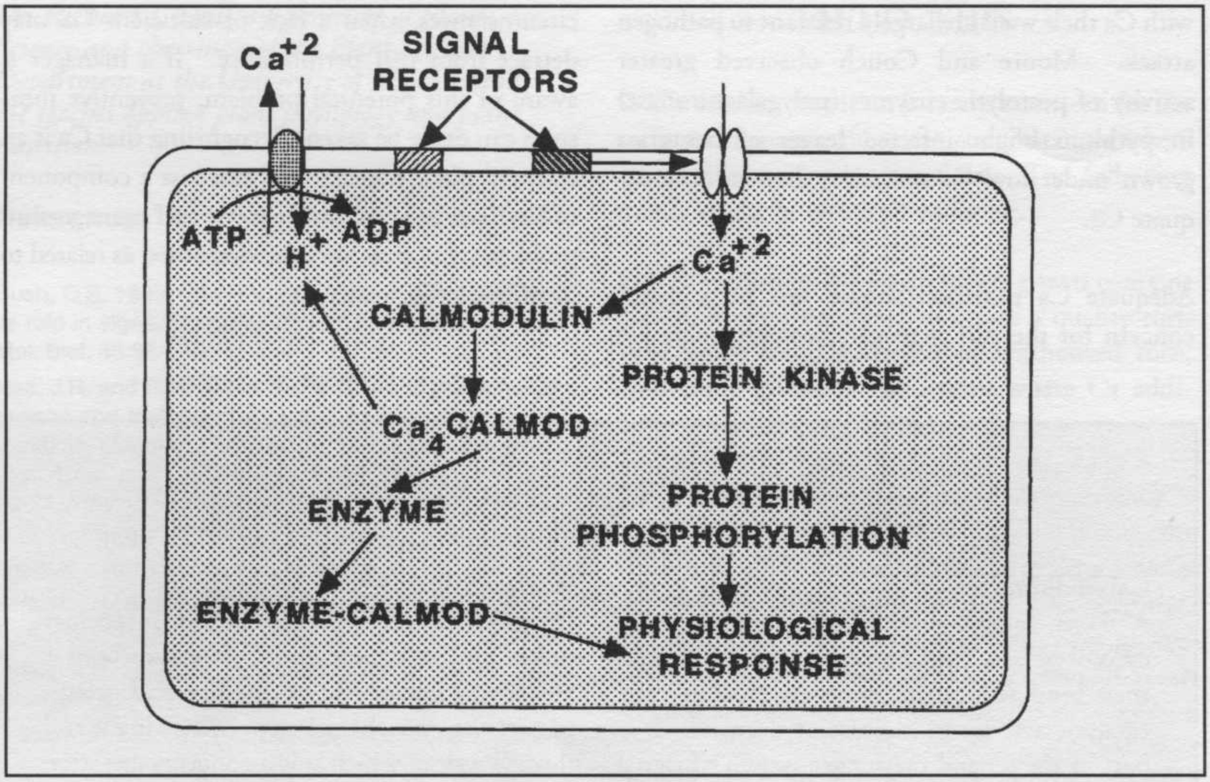

Figure 3. Simplified pathway for signal transduction in a plant cell.

different plants so its validity for turfgrasses is likely.

As mentioned at the outset, Ca is never deficient to plants growing on a well limed or naturally calcareous soil. Consequently insufficient Ca is unlikely to be a problem on roughs, fairways, lawns, athletic fields or utility turfs where mostly native soils are utilized. However, turf managed on synthetic media which contain no soil or on very sandy soil which has not been limed may suffer from low Ca. No field turf will be growing in the complete absence of Ca so classical deficiency symptoms are not likely to be observed. Instead, plants may be inefficient in acquiring nutrients (require high fertility levels) or fail to respond effectively to environmental signals (suffer greater stress injury). These will be subtle effects which only the most perceptive manager will detect. If a sand green requires more fertilizer than normal or if it tends to sustain drought or heat injury when others do not, you might be well advised to check the exchangeable Ca content of the growth medium or have leaf tissue analyzed for total Ca.

A complicating factor may be that turfgrasses differ in their utilization of Ca. Nittler and Kenny found Kentucky bluegrass cultivars to differ widely in their tolerance to low Ca. Thus, a low Ca problem might be unevenly expressed on a site if more than one turfgrass is being grown. A Ca insufficiency would not be my initial diagnosis of a turf problem but you might want to keep it in mind if other more likely solutions fail to provide an answer. Lime is cheap and you are not likely to cause harm by making a judicious application.

One effect of Ca which has been documented on a turfgrass is its impact on disease susceptibility. Colonial bentgrass grown in a nutrient solution deficient in Ca was shown by Moore et al. to suffer greater injury from pythium blight. Plant pathogens frequently initiate infection by producing hydrolytic enzymes that degrade the plant cell wall. The pectin degrading enzyme polygalacturonase is produced by several pathogens as an initial step in the infection sequence. However, calcium pectate is highly resistant to polygalacturonase and when plants are adequately supplied with Ca their walls are largely resistant to pathogen attack. Moore and Couch observed greater activity of pectolytic enzymes (polygalacturonase) in pythium blight infected leaves of bentgrass grown under low Ca nutrition than under adequate Ca.

Adequate Ca nutrition should not be a major concern for the turf manager, however, there are circumstances when a lack of sufficient Ca may detract from turf performance. If a manager is aware of this potential problem, preventive measures can easily be taken. Recognizing that Ca is an essential plant nutrient and not just a component of lime can help minimize some turf management problems that may never be diagnosed as related to insufficient Ca.

TERMS TO KNOW

Calmodulin
A water soluble polypeptide present in the cytosol of cells that can bind 4 Ca^{+2} ions and then bind to specific enzymes causing their catalytic activity to increase or decrease. It is part of the second messenger system of signal transduction in plants and animals.

Cation exchange capacity (CEC)
The number of fixed negative charges in a matrix (soil, cell wall, organic residues) which can attract and bind positively charged cations. Usually expressed as number of charges (mole or millimole) per unit mass (100 grams) of matrix.

Cytosol
The fluid matrix of the cell's cytoplasm. The cytoplasm exclusive of vacuoles, organelles and the nucleus. Much basic intermediary metabolism occurs in the cytosol.

Endomembrane system
A complex system of interconnected membranes within a cell which enclose a specialized space where cell wall polysaccharides are synthesized and modified, proteins are concentrated and polar lipids are constructed.

Pectin
Long chains of galacturonic acid residues linked via an oxygen atom between carbons 1 and 4 of galacturonic acid. The acid groups impart negative charges to pectin giving it and the cell wall of which it is a component cation exchange capacity.

Plasma Membrane
The limiting membrane which encloses the cell protoplast. The surface membrane of a cell which separates inside from outside.

Ppm
Parts per million normally on a weight basis. Milligrams per kilogram and milligrams per liter are both ppm expressions.

Rhizosphere
A zone of soil adjacent to a root that is influenced chemically or biologically by the presence of the root.

Tonoplast
The membrane that encloses the vacuoles of plant cells.

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FIELD TIPS

While calcium nutrition is rarely a concern for the turfgrass manager, there are circumstances where Ca additions may be beneficial. The following points might be worth considering.

1. If the substrate on which turf is grown contains no Ca, it must be added to insure a quality turf. Very sandy soils, reclaimed or synthesized soils, sand-based greens are situations where Ca additions might be considered.

2. Under field conditions, acute Ca deficiency is unlikely. You will not observe growing points collapsing or distorted leaves emerging. More likely you will notice sluggish responses to fertilizer, excessive disease incidence, a tendency for greater stress injury (drought, heat) and a generally weak stand that does not recover well from damage.

3. Calcium is most likely to be deficient in well fertilized grass because its need for Ca will be greater. Stimulated growth and clipping removal will aggravate a chronic Ca insufficiency.

4. Calcium can be added as liming materials (calcium carbonate) and on sandy sites, application should be repeated when shown by soil analysis to be needed, perhaps every two to three years because Ca will leach if there is no cation exchange capacity to retain it in the soil.

5. Foliar spray applications usually are unnecessary and might even cause leaf burn. A Ca source such as lime or gypsum ($CaSO_4$) added to fertilizer or incorporated into topdressing should satisfy grass needs. Calcium nitrate or sulfate are good soluble sources of Ca.

6. Calcium is not likely to become toxic to turfgrasses. Some plants can tolerate Ca salts precipitating around their roots, however, there is much genetic variability in this. As monocots, turfgrasses generally have a somewhat lower Ca requirement than most dicot plants. Excess Ca is more likely to displace needed magnesium and other divalent metal nutrients as well as potassium and that may